Journal of Vegetation Science 15: 615-622, 2004

Subdominant species distribution in microsites around two life forms at a desert grassland-shrubland transition zone

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Abstract

Question: In the same landscape context – at a desert grassland-shrubland transition zone, how does subdominant plant abundance vary in microsites around dominant grasses and shrubs?

Location: Sevilleta LTER, New Mexico, USA (34°21' N; 106°53' W; 1650 m a.s.l.).

Methods: We compared the distribution of subdominant plants in canopy, canopy edge and interspace microsites around individual shrubs (*Larrea tridentata*) and grasses (*Bouteloua eriopoda*) at a transition zone that has been encroached by shrubs within the past 50 - 100 a. Plots of variable size according to microsite type and dominant plant size were sampled.

Results: Subdominant abundance was higher in microsites around *L. tridentata* shrubs than in microsites around *B. eriopoda*. Furthermore, differences in species abundance and composition were higher among microsites around grasses than among microsites around shrubs. The distribution of subdominants was mostly explained by their phenological characteristics, which indicates the importance of temporal variation in resources to their persistence.

Conclusions: This study of coexistence patterns around dominants revealed ecological contrasts between two dominant life forms, but other factors (such as disturbances) have to be taken into consideration to evaluate landscape-scale diversity.

Keywords: Annual; *Bouteloua eriopoda*; Dominant plant; Ecotone; Functional group; *Larrea tridentata*; Scale; Shrub invasion; Spatial heterogeneity.

Nomenclature: Anon. (1999).

Introduction

Many processes determining vegetation pattern occur at the plant scale (Silvertown & Wilson 1994). Often subdominant distribution patterns are affected by the presence of dominant plants, around which microsites with different ecological conditions can be found (e.g. Grime 1998). In arid environments, several studies have related small-scale species coexistence patterns to microsites around dominant plants (e.g. Shmida & Whittaker 1981; Lightfoot 1991; Tielbörger & Kadmon 1997; Pugnaire & Luque 2001). Generally, a marked difference in subdominant species distribution is observed between microsites because of differences in resource availability and the competitive environment (Shmida & Whittaker 1981; Guo 1998). These differences are partially due to positive and negative effects of dominant plants on subdominants (Aguiar & Sala 1994; Tielbörger & Kadmon 2000). Dominant plants with contrasting ecological characteristics, such as grasses and shrubs, may, therefore, influence subdominant species distribution differently (Belsky 1994; Köchy & Wilson 2000). Our objective was to examine the distribution of subdominant species in microsites around dominant grasses and shrubs.

A unique opportunity to study microsites around dominant grasses and shrubs in the same landscape context is offered by transition zones between desert grasslands and shrublands in the northern Chihuahuan desert. At these ecotones the dominant grass, *Bouteloua eriopoda* coexists with shrubs, e.g. *Larrea tridentata*, which have expanded their range within the past 50-100 a (Burgess 1995; Van Auken 2000). Comparing microsites associated with coexisting shrubs and grasses is important, since landscape characteristics, such as the disturbance regime or soil conditions, may influence small-scale coexistence patterns.

Although the distribution of nutrients and water around individual shrubs and grasses has been compared in the northern Chihuahuan desert (Schlesinger et al. 1996; Kieft et al. 1998), it is unclear how different microsites influence subdominant abundance. For grasses (*B. eriopoda*), only community composition has been investigated and little is know about fine-scale coexistence patterns (Huenneke 1996; Kröel-Dulay 1998; Kröel-Dulay et al. 2004). From earlier studies of the influence of shrubs (*L. tridentata*) on subdominant abundance it is unclear if shrubs have negative or positive effects (nurse plant effect) on subdominant species abundance (Shmida & Whittaker 1981; Guo & Berry 1998; Tielbörger & Kadmon 2000; Whitford et al. 2001). Even though the direct comparison of subdominant abundance around dominants promises to increase our understanding of

changes occurring during shrub encroachment, it poses methodological challenges because of the differences in plant sizes.

We expect subdominant species distribution to vary between microsites around *B. eriopoda* and *L. tridentata* because of differences in their morphology, longevity and phenology. *B. eriopoda* is a C_4 perennial grass with a medium life span (ca. 40 a), that has most growth during the summer (Kemp 1983). In contrast, *L. tridentata*, a long-lived (ca. 400 a), evergreen C_3 shrub, typically grows when water is available (Miller & Huenneke 2000). The influence of these ecological characteristics may have different effects on subdominants according to their ecological characteristics. Therefore, we expect different groups of subdominant species with similar morphological, longevity and phenological characteristics to occur in the same microsite(s).

The objective of this study was to study the distribution of subdominant plants in the neighbourhood of individuals of two dominant life forms at a desert grassland-shrubland transition zone. We tested three hypotheses: 1. The abundance of subdominant plants in microsites around *Larrea tridentata* is different from that around *Bouteloua eriopoda*. 2. Around individual plants, subdominant abundance and composition varies among microsites. 3. Subdominant species belonging to the same functional group occur in the same microsite(s).

Methods

Study site

This study was conducted at the Sevilleta Long-Term Ecological Research (LTER) site (http://sevilleta.unm.edu) in central New Mexico (34°21' N; 106°53' W; 1650 m a.s.l.). Mean temperature (1916-1995) at a nearby weather station in Socorro, NM (1398 m a.s.l.), ranges from 2.6 °C in January to 24.6 °C in July; mean annual precipitation is 232 (± 79 SD) mm (Hochstrasser et al. 2002). Domestic livestock has been excluded from the site since 1973.

We selected a transition from *B. eriopoda* grassland to *L. tridentata* shrubland that was free of old roads or fence lines. This transition zone contains kangaroo rat burrows typical of areas where shrubs have recently expanded into grasslands (Krogh et al. 2002). A 100 m × 500 m long transect subdivided into 10 m × 10 m quadrats was located perpendicular to the transition zone. Based on previous studies, we expected that the level of kangaroo rat activity and shrub cover in these quadrats would influence small-scale coexistence patterns (Fields et al. 1999; Guo 1998). To give equal emphasis to all quadrat types independent of their abundance in this particular transition zone, we classified all 500 quadrats into four classes based on the importance of kangaroo rat activity (< 35% or ≥ 35% of quadrats affected) and shrub dominance (*L. tridentata* dominant in < 15% or ≥ 15% of quadrats). A total of 45 quadrats were selected in a stratified random manner for vegetation sampling, such that quadrats with high and low kangaroo rat activity and shrub dominance were represented in similar numbers (Hochstrasser 2001).

Soil texture of microsites

We characterized the surface soil texture (0-7 cm) as an indicator of abiotic conditions. Surface soil texture affects the infiltration capacity of the soil, seed germination and seedling establishment (Lauenroth et al. 1994). Soil samples (5 cm diameter) were collected from four microsites (shrub canopy, shrub canopy edge, grass canopy and in a bare interspace) in 34 of the 45 quadrats selected for sampling vegetation. Because of the small area of the canopy edge of grasses, we did not sample soil texture in this microsite. Each sample was a composite of three subsamples collected from random locations within each microsite in each quadrat. Samples were analysed for texture using a hydrometer method modified for soils with high sand content.

Subdominant abundance

In the 45 quadrats, microsites around a total of 167 *B. eriopoda* and 115 *L. tridentata* individuals were sampled (three randomly selected shrubs and five grasses in each quadrat with a sufficient number of individuals, otherwise as many individuals as available). Groups of shrubs that had overlapping canopies were considered equivalent to an individual. Sampling was conducted in September 1997 at the peak of herbaceous growth.

Around each individual, we distinguished three types of microsites: (1) the canopy – influenced by the above-ground structure of the plant; (2) the interspace – the space between above-ground structures of neighbouring plants of the same species and (3) the canopy edge – a transitional zone between the canopy and the interspace (Fig. 1). The emphasis was placed on delimiting microsite types with different ecological conditions, such that the shape of our sample plots was adapted to the shape of microsites. We sampled the total area of microsites to maximize the area sampled within each microsite. This method was easily adapted to individual plants of different sizes and assured that the scale of sampling corresponded to the scale of plants.

Canopy and canopy edge microsites were defined relative to the edge of a plant canopy (Fig. 1). For shrubs, the canopy microsite included only the area

above which the canopy was multi-layered and shaded the ground for most of the day. We sampled this microsite with a circular plot with a radius of ca. 75% of the radius of the canopy. The shrub canopy edge plot consisted of a ring around the shrub canopy plot. The width of this ring corresponded to twice the remaining distance between the canopy edge and canopy plot, and therefore covered the remaining area under the canopy as well as an area outside the canopy, where the influence of the canopy was still present. For grasses, the perimeter of the canopy microsite corresponded to the perimeter of crowns. We sampled the area delimited by this perimeter and approximated the area of this sample plot with an elliptical shape obtained by measuring the longest diameter of the grass basal cover and the diameter perpendicular to it. For the grass canopy edge, we used a 3 cm wide band around the perimeter of the crowns as the standard delimitation of a plot, because of the presence of grass stems in this area. Therefore, in both shrubs and grasses, the influence of the canopy was expected to be strong in canopy plots and weak in canopy edge plots.

The interspace for both life forms was defined as the area between plants of the same species. Because this microsite could be extensive (several meters), we sampled this microsite with three circles placed immediately adjacent to the canopy edge (Fig. 1). For shrubs, we used three circles with the same radius as the canopy plot. For grasses, the radius of these sample plots was equal to the shorter of the two radii of the canopy ellipse, except in cases where the interspace between grasses was too small; in these cases, we used a plot with the longest radius possible (Fig. 1). Because of size differences between *L. tridentata* and *B. eriopoda*, it was possible for *B. eriopoda* to occur in microsites around *L. tridentata*, whereas only seedlings and small plants of *L. tridentata* occurred in microsites around *B. eriopoda* plants.

In each microsite sample plot, we identified all individual plants by species and counted their abundance (number of plants/microsite). Canopy cover (percent of the sample plot area) was estimated for clonal grasses that could not easily be separated into individual ramets. We converted this cover estimate to a number of grass subunits to allow comparison with the abundance of other subdominant species. For the purpose of deriving the conversion factor, we counted the number of subunits and estimated % cover for a subset of grass plants sampled. These observations indicated that grass subunits increase in size as grass cover increases. An empirical function was fitted to these field observations:

$$S = 0.59 * C^{0.21} \quad (1)$$

where S = size of the subunit and C = cover of the clonal species in the microsite (between 1 and 100). Once the size of the subunit was determined, we converted the cover estimate into a number of subunits by dividing the area occupied by S.

Analyses

Even though shrub density generally increased across the transition zone, the subdominant abundance data from microsites exhibited stationarity (Hochstrasser 2001). The distribution of subdominant plants (excluding seedlings) in microsites was analysed using an approach for different sizes of microsites (Aguiar & Sala 1997; Kröel-Dulay et al. 2000). We calculated the proportion of plants in each type of microsite ($PPLANT_i$) and the proportion of area sampled in this type of microsite ($PAREA_i$):

$$PPLANT_i = IND_i / IND \quad (2)$$
$$PAREA_i = A_i / A \quad (3)$$

where IND_i is the number of individuals found in a given type of microsite, IND is the total number of individuals found in all microsites compared, A_i is the area of a given type of microsite and A is the combined area of all microsites compared. We then performed a Wilcoxon signed rank test to determine if the proportion of plants ($PPLANT_i$) found in the microsite of interest was higher, equal to or lower than expected based on the proportion of area ($PAREA_i$) sampled in this microsite ($\alpha = 0.05$) (Univariate Procedure; Anon. 1988). We selected this method rather than perform a simple calculation of the density of plants because it does not require extrapolation to a standard area. This analysis was performed at two levels of comparison: first, we compared all six microsites in a quadrat and second, we contrasted the three microsites around individual plants.

Hypothesis 1. We used the grouping of microsites within 10 m × 10 m quadrats to compare the abundance of subdominant plants between all microsites represented in a quadrat (grass canopy, grass edge, grass interspace,

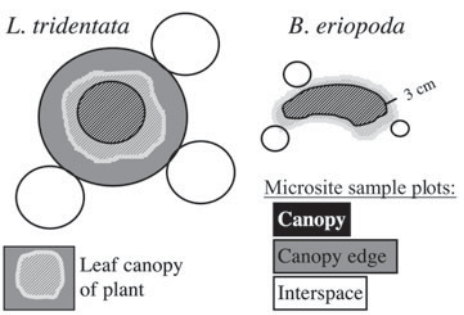

Fig. 1. Sampling plots around *Larrea tridentata* and *Bouteloua eriopoda* individuals, viewed from above.

shrub canopy, shrub edge and shrub interspace). IND_i and A_i in equations (2) and (3) were calculated as the sum over all sample plots from a given type of microsite in a quadrat. Correspondingly, *IND* and *A* corresponded to the sums of all sample plots from all microsites in a quadrat ($n = 45$).

Hypothesis 2. Comparison of microsites around individual plants (canopy, canopy edge and interspace) was used to determine if differences in subdominant species abundance are greater among microsites around shrubs than around grasses. This analysis differed from the previous one in that numbers from microsites around each plant sum to 100%, whereas at the quadrat level, numbers from all six microsites sum to 100%. Numbers from the same type of microsite were aggregated at the plant level: The three interspace plots sampled around each individual were combined to give 'interspace' and small groups of shrubs were considered equivalent to a single shrub. For these groups of shrubs, 'canopy' and 'canopy edge' samples were a composite of samples from three individuals in each group ($n = 115$ for shrubs, $n = 167$ for grasses).

Hypothesis 3. A similar analysis was used to contrast the distribution of functional groups in microsites around individual plants. Subdominant species were classified into functional groups according to their life form (forbs, grasses, subshrubs and succulents), longevity (annual, perennial) and their photosynthetic pathway (C_3, C_4 and CAM). We also analysed the distribution of individual species to determine if species belonging to the same functional group have the same distribution. Only the distribution of functional groups and species which were represented by at least three individuals around at least five dominant plants were taken into consideration. Because of the different areas sampled in each microsite, the number of functional groups or species included in this analysis is not a measure of species richness.

Species composition. One cumulative species list for each microsite was created at the transect level to compare the similarity in species composition among microsites ($n = 1$). Overlap in species lists was determined using Jaccard's Index (J):

$$J = a / (a + b + c) \quad (4)$$

where a is the number of species common to both microsites and b and c are the numbers of species that occur in microsite 1 or 2, respectively (Podani 2000). This index varies between 0 and 1, and expresses the probability that a species will occur in a second microsite, given that it occurred in the first microsite.

Results

Characterization of microsite plots

Sample plots in microsites around *L. tridentata* were larger than in microsites around *B. eriopoda* (Fig. 2a). Canopy sample plots of *L. tridentata* were ca. 0.79 m^2 whereas for *B. eriopoda* they were ca. 0.14 m^2. Interspace samples between *L. tridentata* were larger than the canopy area, whereas interspaces between *B. eriopoda* plants were similar in area to the canopy area. These results partially reflect the way sample plots were designed, but they also indicate differences in the mean size of microsites (Hochstrasser 2001).

Surface soil texture of microsites differed between canopies and interspaces. In shrub and grass canopy, sand content was 77 % whereas the interspace contained 67%. The bare interspace had higher percentages of fine particles (silt 19 %, clay 14%) and large particles > 2 mm (19%) than the canopy areas of both life forms (silt 16 %, clay 8 %, large particles 8 %). The soil texture of the shrub canopy edge was similar to the bare interspace, except for its lower clay content (clay 12%).

Differences in subdominant species abundance and composition around L. tridentata vs. B. eriopoda

Under the *L. tridentata* canopy, we found ca. 19 subdominant plants, whereas in the canopy edge and the interspace more than 74 plants were present (Fig. 2b). In contrast, subdominant abundance was very low around *B. eriopoda* grasses, where less than one individual was found in the canopy and canopy edge and only five individuals in interspaces between plants. Subdominant species abundance in microsites around shrubs was high in comparison to microsites around grasses, even when the area sampled was taken into account (Fig. 2c). On the basis of area sampled, the number of plants in shrub canopy edges and interspaces was greater than expected, whereas it was lower than expected in all grass microsites.

Canopy areas of *L. tridentata* and *B. eriopoda* were more dissimilar (Jaccard's index, $J = 0.3$) than their interspaces ($J = 0.71$) in terms of overall species composition. The lowest species overlap was found when the grass canopy area was compared to shrub microsites ($J = 0.27 – 0.3$).

Differences between canopy, canopy edge and interspace around individual plants

When comparing total subdominant species abundance among microsites around individual plants, we found that the variation in abundance was high around *B. eriopoda*, whereas it was low around *L. tridentata*

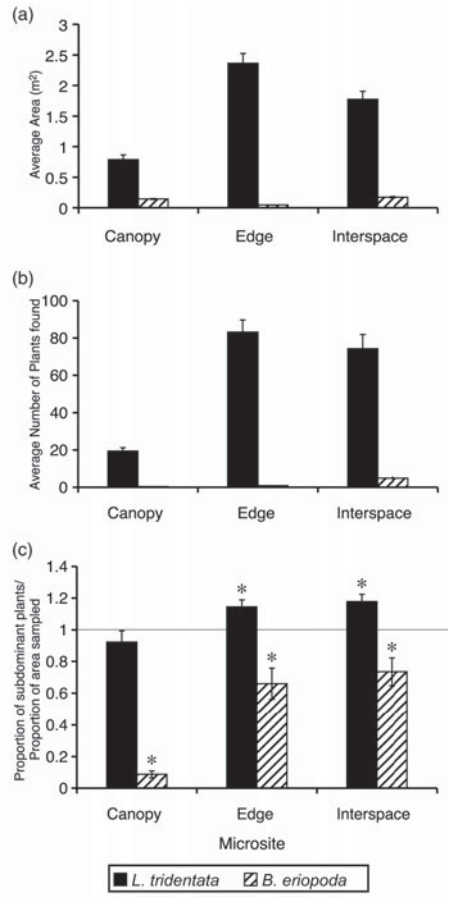

Fig. 2. Comparison of microsites around shrubs (*Larrea tridentata*) and grasses (*Bouteloua eriopoda*). **a.** Mean area of sample plots; **b.** Number of subdominant plants found in sample plots; **c.** Proportion of subdominant plants found/ proportion of area sampled. The * indicates that this ratio is significantly different from 1 (Wilcoxon signed rank test, $\alpha = 0.05$). Error bars are standard errors.

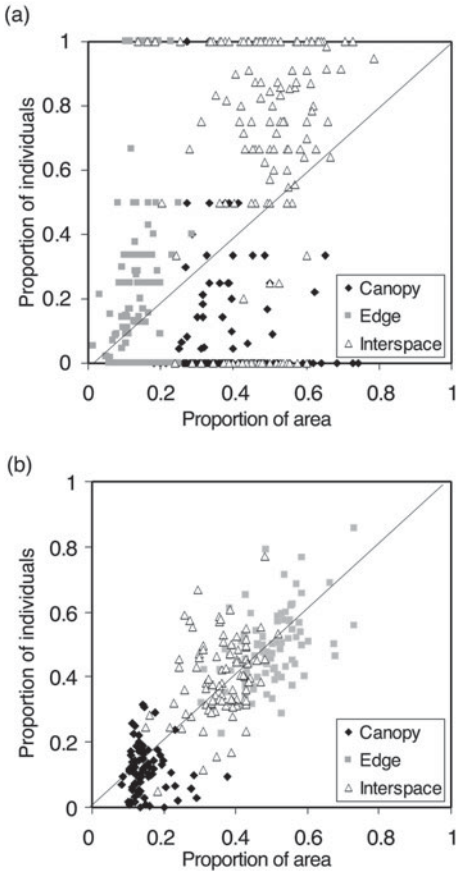

Fig. 3. Comparison of microsites at the individual plant level. Proportion of area sampled versus proportion of subdominant plants found in each microsite. **a.** Microsites around grasses (*Bouteloua eriopoda*) ($n = 167$); **b.** Microsites around shrubs (*Larrea tridentata*) ($n = 115$).

(Fig. 3). For both dominant species, subdominant species abundance was significantly lower than expected based on the area sampled in canopy areas and higher than expected in interspaces. In canopy edges, the abundance of subdominant plants corresponded to the area sampled. Species overlap ranged between 0.41 – 0.58 (Jaccard's index) among grass microsites whereas it was between 0.7 – 0.8 among shrub microsites.

Distribution of functional groups and species in microsites around individual plants.

Functional group responses differed among microsites (Table 1). Near *L. tridentata* C_3 functional groups, except for perennial forbs, were less frequent in interspaces than expected for the area sampled (Table 1). In contrast, C_4 species tended to occur less abundantly under shrub canopies than expected. C_4 perennial forbs and succulents were not sufficiently abundant to compare frequencies among microsites. Not all species which were sufficiently abundant to test hypothesis 3 followed the distribution of their functional group (Table 1). For example, we found that C_4 annual forbs *Chamaesyce* spp. tended to occur in interspaces, whereas *Salsola kali*, another C_4 annual forb, tended to occur under shrub canopies. *B. eriopoda*, a subdominant in microsites around shrubs, tended to be less abundant under shrub canopies than expected based on area.

In microsites around *B. eriopoda*, all functional groups preferentially occurred in interspaces, especially the C_4 annual grasses, which did not occur in the other microsites. C_3 perennial forbs, in particular *Caesalpinia drepanocarpa*, also occurred more frequently than expected in canopy edges. All C_4 perennial grass species showed the same distribution pattern in grass microsites: they occurred more frequently than expected in interspaces.

Table 1. Percentages of subdominant species and functional group abundance in the three microsites around individuals of the dominant species. The last row contains percentages of area sampled in each microsite for comparison. * = significantly lower % of plants in relation to the % area occupied by the microsite; # = a significantly higher percentage (Wilcoxon signed rank test, $\alpha = 0.05$).

Functional group / Species	Shrub canopy	Shrub canopy edge	Shrub inter-space	Grass canopy	Grass canopy edge	Grass inter-space
Total	12 *	48	40 #	8 *	19	73 #
C_3 annual forbs	34	48	18 *			
C_3 perennial forbs	18	48	34	12 *	30 #	59 #
Caesalpinia drepanocarpa	16	47	37	12 *	32 #	56 #
Sphaeralcea wrightii	13	60	28			
Sphaeralcea leptophylla	12	36	52			
Lesquerella fendleri	24	53	22			
C_3 perennial grasses	92 #	8 *	0 *			
C_3 perennial subshrubs and shrubs	33 #	51	16 *			
Gutierrezia sarothrae	36 #	54	11 *			
C_4 annual forbs	12 *	47	41	8 *	10 *	82 #
Chamaesyce serrula	2 *	46	52 #			
Chamaesyce serpyllifolia	3 *	46	51 #			
Chameasyce revoluta	7 *	42	52			
Salsola kali	37 #	47	16 *			
Tidestromia lanuginosa	3 *	50	48			
C_4 annual grasses	3 *	43 *	55 #	0 *	0 *	100 #
Bouteloua barbata	4 *	38 *	58 #	0 *	0 *	100 #
Monroa squarrosa	3 *	52	45			
C_4 perennial grasses	12 *	50	37	8 *	15 *	77 #
Aristida purpurea	22	42	36			
Bouteloua eriopoda	12 *	47	40			
Enneapogon desvauxii	7 *	53	40			
Dasyochloa pulchella	10 *	47	43 #	4 *	4 *	92 #
Muhlenbergia torreyi	19	49	32	0.4 *	15	84 #
Scleropogon brevifolius	13	45	42	0 *	9	91 #
Sporobolus contractus	52 #	34 *	14 *			
Sporobolus flexuosus	25	64	11 *			
% Area	15	50	36	38	14	48

Discussion

Direct comparison of microsites around a dominant shrub (*L. tridentata*) and a dominant perennial grass (*B. eriopoda*) in the same landscape context showed that subdominant abundance was higher near *L. tridentata* than near *B. eriopoda*. Subdominant plants occurred almost exclusively in interspaces around grasses, and differences in subdominant plant abundance were small between microsites around *L. tridentata*. These findings may be related to the direct and indirect effects of the two dominants on abiotic and biotic conditions (e.g. root competition, soils, animals, microbes, microclimate). Furthermore, differences in the characteristics of subdominant plants contribute to this pattern.

Differences in microsite conditions

The abundance of subdominants was higher in all microsites around *L. tridentata* than in microsites around *B. eriopoda*, despite similar soil texture in their canopy areas. In a more extensive study, it was found that, even though soil texture was similar, soil carbon and nitrogen content were higher in soil under *B. eriopoda* than *L. tridentata* canopies (Kieft et al. 1998). Other factors, such as the size of microsites and past disturbances, may explain higher subdominant abundance around *L. tridentata* compared with *B. eriopoda*. Area is an important factor in determining the suitability of microsites for subdominant plants (McConnaughay & Bazzaz 1987; Hook et al. 1994). Alternatively, high subdominant species abundance around *L. tridentata* may be a legacy of past disturbances, especially in recently invaded grasslands (Grover & Musick 1990; Chew & Whitford 1992).

Differences in canopy structure and competitive ability between *L. tridentata* and *B. eriopoda* may also contribute to subdominant distribution around individual plants. The physical presence of above-ground biomass and the strong competitive ability of *B. eriopoda* (Baggs 1997) can exclude subdominant species from the grass canopy. In comparison, shrubs have canopies that do not occupy the same space as subdominant plants, but simply add another layer to the vegetation (Belsky 1994). Shrub canopies can have positive (e.g. shading) as well as negative effects (e.g. interception) on resource availability for subdominant plants (Tielbörger & Kadmon 2000).

Functional groups and subdominant species

Subdominant functional groups, particularly C_3 and C_4 plants, showed contrasting distributions in microsites that may be due to differences in ecological characteristics,

including temperature optima for photosynthesis and nitrogen use efficiency (Gutierrez & Whitford 1987). Temperatures are lower and nitrogen levels higher under shrub canopies than in interspaces (Breshears et al. 1998; Kieft et al. 1998), which may make this microsite particularly suitable for C_3 species (Guo 1998). Similar to a previous study in the Chihuahuan desert (Lightfoot 1991), we found that subdominant abundance was high in interspaces, where summer annuals (C_4) occurred. This contrasts with observations from the Mojave desert, where subdominants (mostly C_3 annuals) tend to occur under shrub canopies (Shmida & Whittaker 1981; Ludwig et al. 1988). Seasonal differences in the activity of C_3 vs. C_4 plants may also be important for coexistence patterns around *B. eriopoda*; C_3 perennial forbs seem to be well suited to co-exist with *B. eriopoda*, a C_4 plant (Kemp 1983; Baggs 1997). Further studies are needed to test if there is a general pattern of distribution of C_3 versus C_4 plants in these microsites.

Even though general patterns of functional group distribution were found, species belonging to the same functional group did not always occur in the same microsites. Species in the same functional group may have functional traits that distinguish them ecologically, such as different constraints on seed dispersal and seedling establishment (Aguiar & Sala 1997; Guo 1998; Bisigato & Bertiller 1999). Furthermore, the suitability of microsites for different species may change over time and their distribution between microsites may shift (Fowler 1988; Primack & ShiLi 1991; Tielbörger & Kadmon 1997).

Implications for landscape-scale diversity

Our results show that subdominant abundance around *L. tridentata* is higher than around *B. eriopoda*, which contrasts with landscape level observations that species diversity is lower in *L. tridentata* shrublands than in *B. eriopoda* grasslands (Huenneke 1996). This discrepancy indicates that our small-scale observations can not be directly extrapolated to the landscape level, because other factors (e.g. disturbances) influence species diversity at the landscape scale (Gosz 1993). Furthermore, this study was conducted at a transition zone where *B. eriopoda* and *L. tridentata* coexist. The presence of these two dominant species may increase landscape level species richness at this transition zone compared to vegetation types with only one dominant (Zólyomi 1987; Łuczaj & Sadowska 1997). Nevertheless, the marked difference in ecological conditions in microsites around plants is an important characteristic of desert ecosystems and contributes to their diversity (Shmida & Whittaker 1981; Guo 1998). Over time, certain microsites may serve as refugia for species when large-scale changes in climate occur (Beatty 1984; Zólyomi 1987).

Acknowledgements. This study was supported by grants from the National Science Foundation to New Mexico State University (DEB-0080412) and to the University of New Mexico (DEB-0080529). T. Hochstrasser was also supported by the U.S. Army ERDC – Construction Engineering Research Laboratory, a scholarship for research and further education from the University of Lausanne, Switzerland and the Francis C. Clark Award for Excellence in Soil Biology from the Natural Resource Ecology Laboratory at Colorado State University. Special thanks to Carry Noteboom and Brian Roeder for help with field work. Phillip L. Chapman provided statistical advice. We thank Tom Stohlgren, Jim Gosz, John Wiens, Bill Parton, Mike Coughenour, György Kröel-Dulay, Katherine Mitchell, Jin Yao, Exequiel Ezcurra and two anonymous reviewers for helpful comments on earlier versions of the manuscript. This is Sevilleta Long-Term Ecological Research Program publication number 297.

References

Anon. 1988. *SAS/STAT User's Guide, Release 6.03*. SAS Inst., Cary, NC, US.

Anon. 1999. *The PLANTS database*. National Plant Data Center. USDA NRCS, Baton Rouge, LA, US. URL: http://plants.usda.gov/

Aguiar, M.R. & Sala, O.E. 1994. Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. *Oikos* 70: 26-34.

Aguiar, M.R. & Sala, O.E. 1997. Seed distribution constrains the dynamics of the Patagonian steppe. *Ecology* 78: 93-100.

Baggs, J.E. 1997. *The role of Bouteloua eriopoda in the community structure and ecosystem function of a semiarid grassland*. M.Sc. Thesis, New Mexico State University, Las Cruces, NM, US.

Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65: 1406-1419.

Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* 75: 922-932.

Bisigato, A.J. & Bertiller, M.B. 1999. Seedling emergence and survival in contrasting soil microsites in Patagonian Monte shrubland. *J. Veg. Sci.* 10: 335-342.

Breshears, D.D., Nyhan, J.W., Heil, C.E. & Wilcox, B.P. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. *Int. J. Plant Sci.* 159: 1010-1017.

Burgess, T.L. 1995. Desert grassland, mixed shrub savanna, shrub steppe, or semidesert scrub? The dilemma of coexisting growth forms. In: McClaran, M.P. & Van Devender, T.R. (eds.) *The desert grassland*, pp. 31-67. University of Arizona Press, Tucson, AZ, US.

Chew, R.M. & Whitford, W.G. 1992. A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosote bushes (*Larrea tridentata*). *J. Arid Environ.* 22: 375-386.

Fields, M.J., Coffin, D.P. & Gosz, J.R. 1999. Burrowing activities of kangaroo rats and patterns in plant species dominance at a shortgrass steppe-desert grassland ecotone. *J. Veg. Sci.* 10: 123-130.

Fowler, N.L. 1988. What is a safe site?: Neighbor, litter, germination date, and patch effects. *Ecology* 69: 947-961.

Gosz, J.R. 1993. Ecotone hierarchies. *Ecol. Appl.* 3: 369-376.

Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86: 902-910.

Grover, H.D. & Musick, H.B. 1990. Shrubland encroachment in southern New Mexico, USA. An analysis of desertification processes in the American Southwest. *Clim. Change* 17: 305-330.

Guo, Q. 1998. Microhabitat differentiation in Chihuahan desert plant communities. *Plant Ecol.* 139: 71-80.

Guo, Q. & Berry, W.L. 1998. Species richness and biomass: dissection of the hump-shaped relationships. *Ecology* 79: 2555-2559.

Gutierrez, J.R. & Whitford, W.G. 1987. Chihuahuan desert annuals: importance of water and nitrogen. *Ecology* 68: 2032-2045.

Hochstrasser, T. 2001. *Pattern and process at a desert grassland-shrubland ecotone*. Ph.D. Thesis, Colorado State University, Fort Collins, CO, US.

Hochstrasser, T., Kröel-Dulay, G., Peters, D.P.C. & Gosz, J.R. 2002. Vegetation and climate characteristics of arid and semi-arid grasslands in North America and their biome transition zone. *J. Arid Environ.* 51: 55-78.

Hook, P.B., Lauenroth, W.K. & Burke, I.C. 1994. Spatial patterns of roots in a semiarid grassland: abundance of canopy openings and regeneration gaps. *J. Ecol.* 82: 485-494.

Huenneke, L.F. 1996. Shrubland and grasslands of the Jornada Long-Term Ecological Research site: desertification and plant community structure in the northern Chihuahuan desert. In: Barrow, J.E., McArthur, E.D., Sosebee, R.E. & Tausch, R.J. (eds.) *Proceedings: shrubland ecosystem dynamics in a changing environment*, pp. 48-50. Intermountain Research Station. USDA Gen. Tech. Rep. Ogden, UT, US.

Kemp, P.R. 1983. Phenological patterns of Chihuahuan desert plants in relation to the timing of water availability. *J. Ecol.* 71: 427-436.

Kieft, T.L., White, C.S., Loftin, S.R., Aguilar, R., Craig, J.A. & Skaar, D.A. 1998. Temporal dynamics in soil carbon and nitrogen resources at a grassland-shrubland ecotone. *Ecology* 79: 671-683.

Kröel-Dulay, G. 1998. Stepwise transformation of phytosociological data: a case study in the semiarid grasslands of New Mexico. *Abstr. Bot.* 22: 95-100.

Kröel-Dulay, G., Hochstrasser, T. & Peters, D.P.C. 2000. The influence of kangaroo rat mounds on species diversity and abundance in two grassland types at a semi-arid ecotone. *85th Annu. Meet. Ecol. Soc. America. Symp. Abstr.,* p. 300.

Kröel-Dulay, G., Ódor, P., Peters, D.P.C. & Hochstrasser, T. 2004. Distribution of plant species at a biome transition zone in New Mexico. *J. Veg. Sci.* 15: 531-538.

Krogh, S.N., Zeisset, M.S., Jackson, E. & Whitford, W.G. 2002. Presence/absence of a keystone species as an indicator of rangeland health. *J. Arid Environ.* 50: 513-519.

Köchy, M. & Wilson, S.D. 2000. Competitive effects of shrubs and grasses in prairie. *Oikos* 91: 385-395.

Lauenroth, W.K., Sala, O.E., Coffin, D.P. & Kirchner, T.B. 1994. The importance of soil water in the recruitment of *Bouteloua gracilis* in the shortgrass steppe. *Ecol. Appl.* 4: 741-749.

Lightfoot, K.S. 1991. *Association of annual plants and shrubs in the northern Chihuahuan desert*. M.Sc. Thesis. New Mexico State University, Las Cruces, NM, US.

Łuczaj, A. & Sadowska, B. 1997. Edge effect in different groups of organisms: vascular plant, bryophyte and fungi species richness across a forest-grassland border. *Folia Geobot. Phytotax.* 32: 343-353.

Ludwig, J.A., Cunningham, G.L. & Whitson, P.D. 1988. Distribution of annual plants in North American deserts. *J. Arid Environ.* 15: 221-227.

McConnaughay, K.D.M. & Bazzaz, F.A. 1987. The relationship between gap size and performance of several colonizing annuals. *Ecology* 68: 411-416.

Miller, R.E. & Huenneke, L.F. 2000. Demographic variation in a desert shrub, *Larrea tridentata*, in response to a thinning treatment. *J. Arid Environ.* 45: 315-323.

Podani, J. 2000. *Introduction to the exploration of multivariate biological data*. Backhuys, Leiden, NL.

Primack, R.B. & ShiLi, M. 1991. 'Safe sites' for germination using *Plantago* seeds: a repetition of a thrice-published experiment. *Bull. Torrey Bot. Club* 118: 154-160.

Pugnaire, F.I. & Luque, M.T. 2001. Changes in plant interactions along a gradient of environmental stress. *Oikos* 93: 42-49.

Schlesinger, W.H., Raikes, J.A., Hartley, A.E. & Cross, A.F. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* 77: 364-374.

Shmida, A. & Whittaker, R.H. 1981. Pattern and biological microsite effects in two shrub communities, Southern California. *Ecology* 62: 234-251.

Silvertown, J. & Wilson, J.B. 1994. Community structure in a desert perennial community. *Ecology* 75: 409-417.

Tielbörger, K. & Kadmon, R. 1997. Relationships between shrubs and annual communities in a sandy desert ecosystem: A three-year study. *Plant Ecol.* 130: 191-201.

Tielbörger, K. & Kadmon, R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81: 1544-1553.

Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. *Annu. Rev. Ecol. Syst.* 31: 197-215.

Whitford, W.G., Nielson, R. & de Soyza, A. 2001. Establishment and effects of establishment of creosotebush, *Larrea tridentata*, on a Chihuahuan Desert watershed. *J. Arid Environ.* 47: 1-10.

Zólyomi, B. 1987. Coenotone, ecotone and their role in preserving relic species. *Acta Bot. Hung.* 33: 3-18.

Received 9 January 2003;
Accepted 22 March 2004.
Co-ordinating Editor: E. Ezcurra.